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ON THE MECHANISM OF THE MOVEMENTS OF THE IRIS. By J. N. LANGLEY, M.A., F.R.S., AND H. K. ANDERSON, M.A., M.B.

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ON THE MECHANISM OF THE MOVEMENTS OF THE IRIS.

By J. N. LANGLEY, M.A., F.R.S., *Trinity College*, AND H. K. ANDERSON, M.A., M.B., *Caius College, Cambridge.*

CONTENTS.

THE cause of the dilation of the pupil, which is produced by stimulating the cervical sympathetic, has been a subject of controversy for the last fifty years, and there is perhaps more difference of opinion on the matter now than there was in the time of Budge and Waller.

So much has been written on the subject, that it would have been far simpler for us to have confined ourselves to giving an account of the facts which we are able to add to those previously known; but with a subject of such complexity, we could hardly hope to do much towards the settlement of the controversy without taking into consideration the varied views which have been put forward. We accordingly deal with all the facts and arguments of any importance with which we are acquainted.

Anæsthetics used. In all our experiments anæsthetics were used, and primarily chloral for the rabbit, chloroform for the cat, and morphia for the dog; after these had taken effect, a mixture of absolute alcohol, chloroform and ether was given at intervals with the inspired air.

THEORIES AS TO THE CAUSE OF THE DILATION OF THE PUPIL.

In giving a brief summary of the theories which have been, or which might be, put forward with any plausibility to explain the dilation of the pupil, we shall for the present mention those only which deal with dilation produced by stimulating the sympathetic. For this lies at the root of the matter, and the view taken as to the dilation produced in other ways will necessarily depend upon what is shown to be the cause of the sympathetic dilation. The theories to be considered are :—

1. That dilation is due to the action of the sympathetic vaso-constrictor nerves. Grünhagen has perhaps been most concerned in bringing this theory into prominence. There are two ways in which the contraction of the blood-vessels of the iris, induced by the vaso-constrictor nerve-fibres, might bring about dilation of the pupil.

(*a*) By decreasing the quantity of blood in the iris, so that it shrinks. This appears to be the method implied by the upholders of the theory.

(*b*) By a longitudinal contraction of the radial arteries of the iris; this contraction dragging the sphincter outwards. A marked longitudinal muscular coat has been described in some animals in the arteries of the iris.

2. That dilation of the pupil is caused by the contraction of radially arranged muscular fibres. This view has been taken by Budge, Henle and many others.

3. That dilation of the pupil is caused by inhibition of the sphincter muscle. Grünhagen and Samkowy[1] (1875) stated as a possibility that the sympathetic might be an 'Erschlaffungsnerv' of the sphincter, but Grünhagen left the matter there, and appears to have adhered to the vascular theory. François-Franck[2] (1880) expressed his opinion, though not without reserve, that the sympathetic dilator nerves of the iris act in the same manner as the dilator nerves of the vessels, and suspend the activity of the constrictor nerves. Gaskell[3] (1886) more definitely put forward the inhibitory theory, and since then it has found a good deal of support. The theory of course requires the presence of elastic tissue in the iris, which is more or less stretched except when the pupil is dilated to its full extent.

It is conceivable that the sphincter should aid in the dilation of the pupil by actively elongating, but this view has not, so far as we know, been advanced.

4. It is possible that in certain circumstances, a certain degree of dilation of the pupil should be caused by a relaxation of the ciliary muscle. By such relaxation the elasticity of part of the ciliary region and the anterior part of the choroid would come into play, and pull backwards the iris.

[1] Grünhagen u. Samkowy. *Arch. f. d. ges. Physiol.* x. p. 165, 1875.

[2] François-Franck. *Travaux de Laboratoire de M. Marey*, iv. p. 55, 1880.

[3] Gaskell. This *Journal*, vii. p. 38, 1886 and *Proc. Physiol. Soc.* 1887, p. xxxi. (This *Journal*, ix. 1888.)

5. Lastly, the dilation of the pupil might be due to the simultaneous action of more than one of the above causes.

On reviewing the evidence which has been brought forward in favour of one or other of the above-mentioned theories, we do not find that it is in any case conclusive. This, indeed, was to be expected, for when opposite opinions are held with equal positiveness by competent observers, it is commonly safe to believe, that the opinions are the outcome of individual bias acting on inconclusive evidence. We give first a critical account of the experimental proofs which have been given for and against the existence of a dilator muscle in the iris.

The histological question we leave for a later paper. We do this with the less hesitation, since even if we satisfied ourselves of the presence of radial unstriated muscle-fibres in the iris of the cat and dog, it would still remain to be shown, that their function is to cause dilation of the pupil, and that the sympathetic sends motor fibres to them. As Grünhagen has more than once insisted, radial muscle-fibres might serve to draw towards the pupil the ciliary part of the iris, provided the sphincter muscle, when contracted, were sufficiently strong to serve as a fixed point.

Alleged proofs of a dilator muscle in the iris.

1. **Asserted death of the sphincter before the dilator muscle.** Budge[1] (1855) considered that he had shown conclusively that a dilator muscle exists. He asserted that soon after general death, the sphincter muscle dies. Since, as was found by M. E. Weber, stimulation of the eye causes dilation for some time after death, Budge concluded that the dilation could only be due to a dilator muscle. His proof of the death of the sphincter is not very clear, and need not be gone into, for it is certain that the sphincter does not die soon after general death. Indeed, as Brown-Séquard[2] (1859) has shown, the sphincter can be made to contract one to three days after the death of the animal.

2. **Constriction or dilation of the pupil according to the position of the stimulating electrodes.** Bernstein and Dogiel[3] found that the pupil of a recently killed animal could be made larger or smaller at will by varying the method of stimulating the eye. When

[1] Budge. *Ueber die Bewegung der Iris* (Braunschweig), 1855, p. 185.

[2] Brown-Séquard. *Journ. de la Physiologie*, T. II. p. 289, 1859.

[3] Bernstein und Dogiel. *Verhandl. d. naturhist.-med. Vereins zu Heidelberg*, Bd. IV. ii. 1865 and also Bernstein *Zeitschrift f. rat. Medicin*, Bd. XXIX. p. 35, 1867.

two electrodes, connected with the secondary coil of an induction machine, were placed opposite one another at the junction of the cornea

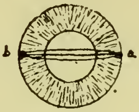

FIG. 1.

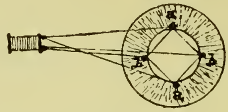

FIG. 2.

and sclerotic, as in Fig. 1, the pupil dilated. This indeed had been previously observed by Budge and others. But when four electrodes were taken, two from each pole of the secondary coil, and these were placed on the cornea above the sphincter edge of the iris in the manner given in Fig. 2, a contraction of the pupil was obtained.

Bernstein and Dogiel argued from the laws of the distribution of the electric current that with the one position of the electrodes, the current would be such as to stimulate chiefly a radially arranged muscle; and with the other position of the electrodes, the current would be such as to stimulate a circularly arranged muscle; and they concluded that a radial dilator as well as a circular sphincter muscle must be present.

On similarly stimulating the eyes of living animals, Bernstein and Dogiel found the results to be inconstant, probably on account of reflex effects caused by stimulating sensory branches of the fifth nerve.

Engelhardt[1] repeated and confirmed the experiments of Bernstein and Dogiel, but states that he obtained constant results in living as well as in recently killed animals (rabbits and dogs).

The common occurrence, in the given conditions, of the results just mentioned is easy of observation, although in the rabbit the movements of the iris are apt to be very sluggish. We do not however find that they are constant, the 'central' stimulation not infrequently causes dilation of the pupil, the 'peripheral' stimulation may cause a preliminary constriction. The conditions which cause these variations, we have not been at pains to determine; for the method of experiment is not one likely to decide the question of the existence of a radial muscle. The difference in the effect of peripheral and central stimulation might be explained on either the vaso-motor or on the inhibitory theory. For the peripheral stimulation is clearly that which is most adapted to cause contraction of the blood-vessels of the iris; and for any proof we

[1] Engelhardt. *Unters. a. d. physiol. Lab. in Würzburg*, Hf. IV. p. 299, 1869.

have to the contrary, it may be that which is most adapted to cause inhibition of the sphincter muscle.

3. **Local dilation of the pupil.** Budge and Waller[1] (1852) noticed in the rabbit that for a certain time after death, the pupil became elliptical when electrodes were placed on opposite sides of the edge of the cornea; and if one electrode was moved farther from the iris, the pupil was at this electrode less dilated. The elliptical shape of the pupil was produced by Engelhardt (*op. cit.* 1869) on living rabbits.

Hensen and Völkers[2] (1868) found local dilation of the pupil on stimulating a single ciliary nerve.

Jessop[3] (1885) states that in the human eye, if the cornea and conjunctiva be dried, and cocaine be placed upon a limited portion of it, dilation of the pupil will first take place in the segment adjoining this portion.

Jegorow[4] (1886) found in the dog that stimulation of a single long ciliary nerve causes local dilation of the pupil; on section of all save one ciliary nerve, the pupil does not contract equally in all parts, and then on stimulation of the cervical sympathetic, or of the central end of a sensory nerve, a marked local dilation takes place.

We have made one or two experiments in the manner of Jegorow; sometimes obtaining similar results, and sometimes—like François-Franck—on stimulating a single ciliary nerve obtaining general dilation or general constriction. This method of experiment is troublesome, and for our ends offers no advantage over that of stimulating the sclerotic, so that we did not pursue it further.

A local dilation of the pupil can be obtained with little trouble by placing the stimulating electrodes on the sclerotic. We have usually cut through the conjunctiva, so as to make a greater extent of the sclerotic accessible. The strength of current required varies a good deal; sometimes a weak current is sufficient. A local dilation can be obtained by stimulating almost any part of the sclerotic, but as it is generally most local when the electrodes are 1 to 2 mm. from the edge of the cornea, we have generally stimulated in that region, and have placed the electrodes so that they are in a line with a radius of the pupil. The maximum dilation is not always exactly in a line with the

[1] Budge et Waller. *Comptes Rendus de l'Acad. d. Sciences*, T. XXXIV. p. 164, 1852.

[2] Hensen u. Völkers. *Henle's Jahresbericht* 1868, p. 483 (*Experimentaluntersuchungen ü d. Mechanik der Accommodation.* Kiel, 1868).

[3] Jessop. *Proc. Royal Soc.* Vol. XXXVIII. p. 432, 1885.

[4] Jegorow. *Arch. f. Anat. u. Physiol.* (Physiol. Abt.) 1886, p. 149.

electrodes, especially when the electrodes are not close to the edge of the sclerotic, this depends no doubt upon the distribution of nerves in the sclerotic and choroid.

The local dilation is unequally marked in different animals; in the rabbit the dilation is least local; the pupil enlarges more or less considerably, although the part opposite the electrodes dilates more than

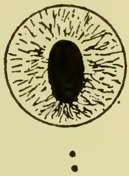

Fig. 3.

Fig. 4.

Fig. 5.

Diagrams of local dilation of the pupil caused by local stimulation of the sclerotic. The two dots outside the iris show the position of the stimulating electrodes. The process of reproducing the drawings has caused the lower part of the pupil in Fig. 3 to be irregular in outline instead of smooth, and to be a trifle too wide, and in Fig. 4 to appear to run to a point instead of being rounded.

the rest; moreover the locally dilated portion is much rounded (cp. Fig. 3). As a rule too the movement is sluggish. In the cat, the increase in the size of the pupil is less, and the locally dilated part is more pointed; since the pupil of the cat is generally large when chloroform alone has been given, it is advisable to give morphia also, or to apply locally a little pilocarpin or eserin. In the dog the local dilation (Fig. 4) is perhaps even better marked than in the cat; in favourable circumstances, when the electrodes are moved round the edge of the sclerotic, the iris flows, as it were, after the electrodes; when the pupil is strongly contracted from morphia, stimulation of the sclerotic gives a small pointed dilation (Fig. 5). After injection of atropin into a blood-vessel, the local dilation lasts long after the removal of the stimulus, no doubt in consequence of the diminution in tone of the sphincter muscle.

We have modified the form of the experiment by stimulating simultaneously different parts of the sclerotic with three or four pairs of electrodes; in such case there is a local dilation at each, opposite each spot stimulated, and the pupil takes very irregular forms. We give as illustration Fig. 6, showing successive changes in the pupil of the cat. The two dots external to the circle indicate the position of the stimulating electrodes; (I) shows the normal pupil, (II) on applying the first pair of electrodes, (III) on applying a second pair of electrodes,

(IV) on applying a third pair of electrodes; (V) on removing the third pair of electrodes to another spot.

A local dilation has been taken without much inquiry as proof of the existence of a dilator muscle. It is clear, however, that if a general contraction of the blood-vessels of the iris could cause a general dilation

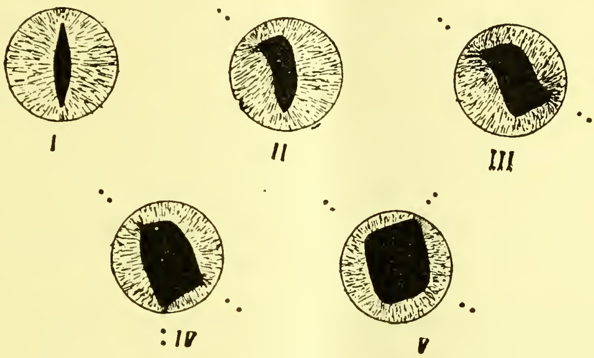

FIG. 6.

of the pupil, a local contraction of the blood-vessels could cause a local dilation of the pupil. As regards the inhibitory theory, it has been assumed that a local inhibition of the sphincter muscle would cause a general, and not a local dilation of the pupil, and the pupil would remain round. But the assumption appears to be unfounded. We have constructed a model to show this.

Two concentric circles are drawn on a board, and sixteen equidistant radii drawn. Holes are made where the radii cut the circles, and pegs made to fit the holes. Sixteen india-rubber threads of equal elasticity and extensibility represent the radial elastic part of the iris, these at one end are fixed to the pegs, and at the other they are fixed, at equal distances from one another, to a central india-rubber ring which represents the sphincter. With this arrangement the central elastic ring forms a regular symmetrical figure whether the pegs are placed in the inner or the outer circle. On the inhibitory theory of the movements of the iris, a portion of the sphincter which is inhibited will be more easily extensible. This can be represented on the model by making a portion of the central india-rubber ring smaller than the rest; or by substituting for it another, specially made, with a given portion (say $\frac{1}{16}$) of smaller diameter than the rest. In such case, when the pegs are put in the holes, and so the central ring stretched, the weaker portion of the ring is drawn farther from the centre, and within limits

the greater the radial tension the greater the irregularity of the central figure.

A regular, approximately circular (sixteen sided) central figure, can be obtained by shifting the central attachments of the radial threads, so that they are equidistant in the stretched state of the central ring, but this condition does not correspond to anything that can be obtained in the iris, for the central attachments of the radially arranged tissue of the iris cannot shift along the sphincter edge.

A certain amount of local dilation of the pupil might, then, be produced by a local inhibition of the sphincter muscle. We do not think that the irregular forms of the pupil which can in fact be produced (cp. above, Fig. 6) are capable of being explained in this way, but since the evidence did not promise to be the simple and conclusive evidence we were looking for, we have not proceeded further upon these lines.

4. **Dilation after removal of the sphincter muscle.** Kölliker[1] in 1855 gave the results of three experiments on rabbits. The rabbits were killed, the cornea removed, and the inner (pupillary) portion of the iris cut away. In two of the animals the remaining part of the iris was stimulated directly, in the third the cervical sympathetic was stimulated; in all three animals there was distinct dilation of the artificial pupil. Kölliker satisfied himself by microscopical examination that in each case the whole of the sphincter had been removed.

It is curious how little attention has been paid to these experiments; taking them as they are given, they make a very strong case for the occurrence of dilation of the pupil apart from inhibition of the sphincter. Two objections might be urged against them. It might be said that the whole of the sphincter was not removed; it is to be supposed that those who adopt the inhibitory theory are of this opinion, but in face of Kölliker's statement about it, and of the fact that the sphincter in the rabbit is not described by anyone as stretching far from the pupillary border, the opinion requires justification. A second objection which might be made is that the dilation of the pupil was produced mechanically by the projection of the lens. When the cornea is removed, any pressure on the globe of the eye will cause projection of the lens and a widening of the pupil (unless the sphincter is very strongly contracted), and a pressure on the globe of the eye can be produced reflexly through the third nerve on direct stimulation of the iris, and directly by the smooth muscle of the orbital membrane on stimulation

[1] Kölliker. *Zeitsch. f. d. wissensch. Zool.* Bd. vi. p. 143, 1855.

of the sympathetic. Kölliker does not mention that he was on his guard against this source of error.

In any case, the experiments do not necessarily show the existence of a radial muscle, for the results are capable of being explained by a shortening of the arteries of the iris.

We have repeated Kölliker's experiments in various animals; as they involve removal of the cornea it will be convenient to give here the effects of this removal, and the effects of varying the pressure in the anterior chamber.

Effect of varying the pressure in the anterior chamber of the eye, and of removal of the cornea. It has long been known[1] that tapping the anterior chamber or removal of the cornea causes a narrowing of the pupil.

When the point of a Pravatz syringe is passed through the edge of the cornea into the anterior chamber and the fluid is withdrawn, the pupil contracts; the contraction is slower in the rabbit than in the cat; on re-injecting the fluid withdrawn, the pupil again dilates, but usually not to its original extent and sometimes great pressure has to be exercised before any considerable dilation occurs, and this is especially the case in the rabbit. In the rabbit as the fluid is withdrawn, the lens and iris come forward and eventually touch the cornea, the cornea as a rule remaining smooth; in the cat the cornea usually becomes folded when much aqueous humour is withdrawn. The difference depends upon the stouter nature of the sclerotic in the cat, whereby it yields less readily to external pressure.

After removal of much aqueous humour, the enlargement of the pupil on stimulating the sympathetic—and also on stimulation of the sclerotic—is surprisingly less than normal, and in the rabbit it may be barely perceptible. On increasing the pressure in the anterior chamber by injecting warm normal salt solution, the dilating action of the sympathetic increases in most cases, but it is rarely restored to normal; the normal action is however restored, when the eye is left for an hour or two.

The effect of removing the cornea is like that of removing the aqueous humour; the pupil in the rabbit contracts until it is but $1\frac{1}{2}$ to 2 millimetres in diameter; in the cat, the pupil contracts greatly but commonly is not reduced to a slit. The edge of the iris fits closely upon the lens, so that a certain amount of fluid is retained in the

[1] Cp. Budge. *Ueber d. Bewegung der Iris*, 1855, p. 63.

posterior chamber. On lifting the edge of the iris a portion of the fluid runs out. The diminution in the extent of the 'sympathetic' dilation, caused by removing the cornea, is very great in the rabbit and considerable in the cat; in the rabbit, the dilation may be barely perceptible, and commonly ceases to be visible in a very short time.

The contraction of the pupil which ensues on removing the cornea is chiefly due to a contraction of the sphincter; as noticed by Grünhagen[1] when the sphincter edge of the iris is cut round it contracts still farther. The varying degree of contraction of the muscle in different cases accounts in the main for the somewhat varying effects of increasing and decreasing the pressure in the anterior chamber, and of removing the cornea, which we have spoken of above, and explains in part the diminished effect of stimulating the sympathetic in these circumstances.

Budge (*op. cit.* p. 64) states that atropin, instilled into the eye in the rabbit, does not diminish the effect which removal of the cornea has on the size of the pupil. We have injected atropin into the blood, and find in all cases that subsequent removal of the cornea leads to less contraction of the pupil than normally, and especially in the cat. Thus in the cat, on withdrawing and replacing the aqueous humour with a syringe, the iris may flap up against the cornea, otherwise barely changing; and on removing the cornea, the pupil may remain wide. This we have also seen after the injection of 50 mgs. of nicotin. On the other hand atropin only slightly enlarges the exposed iris. The decrease in the size of the pupil, caused by removing the cornea, is less some hours after death, and is but slight when the irritability of the sphincter ceases, i.e. about two days after death.

We conclude, then, that the exposed sphincter contracts partly in consequence of a stimulation of its nerve-endings and partly in consequence of a direct action upon its muscular substance. Why the latter stimulation should, after injection of atropin or nicotin, be sometimes so slight, is not clear.

Of course mechanical causes also modify the size of the pupil; increased pressure in the anterior chamber, which forces backward the ciliary region of the iris, increases the size of the pupil; diminished pressure, which allows the ciliary region of the iris to come forward, and the anterior surface of the iris to be less curved, decreases the size of the pupil (cp. diagram, Fig. 7). Bulging of the lens, carrying forward the

[1] Grünhagen. *Arch. f. d. ges. Physiol.* x. p. 172, 1875.

sphincter edge of the iris, causes dilation, a dilation of this kind is often seen in the exposed iris on stimulating the third nerve. If in a cat, in which the pupil is dilated by chloroform, a needle be passed through the edge of the cornea, and the lens pressed back, the pupil at once becomes smaller, enlarging again as the pressure on the lens is relaxed[1]. In

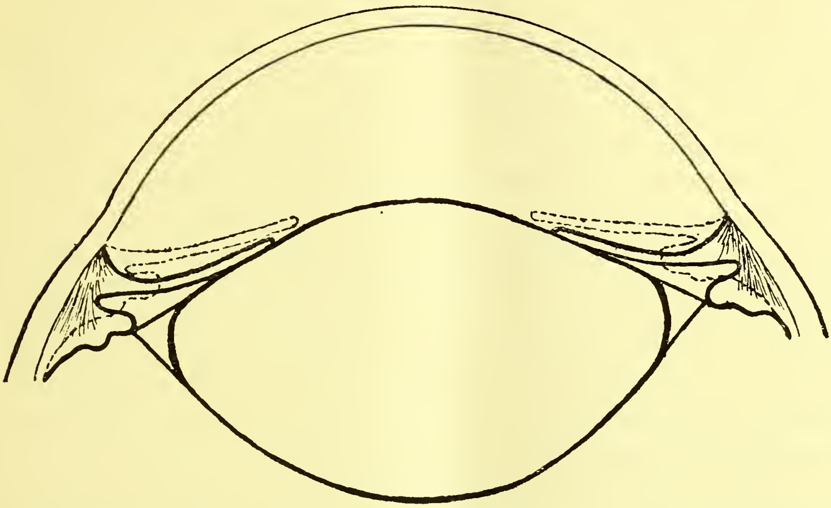

FIG. 7. Diagram to show how variations in the pressure in the anterior chamber mechanically produce variations in the size of the pupil.

addition, there may be, especially in the rabbit, a diminution in the size of the pupil on removing the cornea, in consequence of the sclerotic at the line of attachment of the iris being less distended, so that the circumference of the iris is diminished.

As shown by Budge a loss or an imbibition of fluid causes, several days after death, some increase or decrease in the size of the pupil; this, no doubt, is purely mechanical.

We have said above that after withdrawing with a syringe the aqueous humour from the anterior chamber, stimulation of the sympathetic often produces a very slight effect. There is one source of error which requires notice; if the iris is punctured so that there is even a trifling escape of blood, the aqueous humour may clot, and the clot prevent or reduce the sympathetic dilation of the pupil. It may be mentioned also that when the point of the syringe is kept in contact with the iris, a film forms over the iris, in the part of the aqueous

[1] After a few repetitions the sphincter usually contracts, and the pupils become slit-shaped.

humour lying immediately over it, so that the needle becomes adherent to the iris. The film so formed may almost entirely prevent the dilation of the pupil.

On cutting off the cornea, the ocular muscles lose a part of their tone, so that, on turning the side of the head downwards, the eye protrudes considerably from the orbit.

In contrast to the removal of the aqueous humour, removal of the vitreous humour has a comparatively slight effect on the sympathetic dilation. In the cat, a considerable portion of the vitreous humour may be removed and the sympathetic will still cause nearly maximal dilation; wide dilation may also be obtained even after removal of the lens.

Turning now to Kölliker's experiment on the rabbit; if the inner (pupillary) third of the iris be quickly removed and the sympathetic stimulated there is a slight movement of the iris; to obtain it again the iris should be brushed towards the centre of the lens so as to extend it radially; as a rule however the sympathetic soon becomes ineffective. The movement of the iris is commonly so slight, that the experiment, taken by itself, is anything but convincing that the normal wide dilation is produced by the contraction of a radial muscle.

In the cat and dog, after removal of the inner half of the iris, the sympathetic causes a very marked dilation of the artificial pupil. A movement is still visible after two-thirds of the iris has been cut away. The movement is generally better seen in the cat than in the dog. In all cases it is best to extend the peripheral portion of the iris by brushing it towards the centre of the lens. The duration of the sympathetic action is very variable, in some cases we have obtained no effect after the first few minutes, in others it has been obvious for half-an-hour to an hour.

Alleged proofs of the absence of a dilator muscle.

The experimental proofs which have been brought forward as to the absence of a dilator muscle come mainly from Grünhagen and his pupils.

1. **The comparative behaviour of the pupillary and ciliary portions of the iris.** There are two effects to be considered here (*a*) that of temperature and (*b*) that of electrical stimulation.

(*a*) *Temperature.* Interesting observations on the effect of temperature on the iris were made by Brown-Séquard[1] in 1859. He cooled or warmed the cut-out eye as rapidly as possible. In mammals,

[1] Brown-Séquard. *Journ. de la Physiol.* II. p. 291, 1859.

his results, so far as it is necessary to quote them, were: that contraction of the pupil was caused by warming or cooling, provided the change of temperature was considerable and rapid; that when the pupil was contracted owing to warmth or cold, it dilated on being cooled or warmed. Both contraction and dilation were slow.

Samkowy[1], under Grünhagen's direction, found that the cut-out sphincter iridis of mammals slowly contracted when gradually warmed, and slowly dilated when gradually cooled. In the excised ciliary part of the iris, on the other hand, he found no shortening when a radial strip was warmed.

Grünhagen caused similar experiments to be made, with an improved form of apparatus[2].

We have simply taken the iris or its pupillary portion, or its ciliary portion, placed it in sodium chloride solution ·6 p.c. at 15° C. and at 35° C. and noted its behaviour.

Behaviour of the whole iris in normal salt solution. The iris from a recently killed animal is pinned out over a ring of cork,—or the anterior half of the eye is taken, the cornea removed, and the sclerotic pinned out on a ring of cork—and placed in salt solution at about 15° C.[3] The pupil is then of medium size, and the tone of the sphincter not great though somewhat variable; if the pupil is artificially dilated and distorted, it only slowly returns to its original size. On placing the iris in salt solution at about 35° C., the pupil rapidly narrows and becomes very small; if it is enlarged and distorted artificially, it rapidly returns to its small size. On re-placing the iris in the cool salt solution the tone of the sphincter quickly disappears, the dilation of the pupil is not great, unless the iris has been much stretched on pinning it out; but on distorting the pupil it only slowly returns to its normal shape. A constriction or partial relaxation can thus be obtained a considerable number of times. A constriction of the pupil when the iris is placed in warm salt solution can be observed in the rabbit, cat and dog 36 to 48 hours after the death of the animal, if the eye has been left in the body at a temperature of 16° to 20° C. But the longer after death, the less does the sphincter lose its tone on transferring it from the warm to the cool salt solution; and a certain time after death the sphincter once

[1] Samkowy. *Arch. f. d. ges. Physiol.* ix. p. 399, 1874.

[2] Cp. Grünhagen. *Archiv f. d. ges. Physiol.* Bd. xxxiii. p. 59, 1884.

[3] The iris in salt solution at 0°—3° C. behaves the same way as in salt solution at 15° C. except that, perhaps, it becomes flabby more quickly. We have not observed any certain preliminary contraction of the pupil on placing the iris in salt solution at 0° C.

contracted gradually loses its tone and is comparatively little affected by subsequent changes in the temperature of the salt solution.

Behaviour of the sphincter in normal salt solution. When the sphincter ring of the iris is removed and cut through so that it forms a single strip, it can be extended to a long thread in cold salt solution, and if left to itself, only slowly shortens and only partially. If this extended thread be dropped into warm salt solution, it at once contracts, forming a small clump; if again extended, it regains its previous condition quickly when the extending force ceases. The effect of subsequent cooling and warming varies, as with the whole iris, with the time after death at which it has been obtained.

Behaviour of the ciliary portion of the iris. When the ciliary portion of the iris is cut out, stretched in cool salt solution, and then dropped into warm salt solution there is very little longitudinal shortening; if there is much, it indicates the presence of a portion of the sphincter muscle. In the cat and dog, the sphincter occupies half or more than half of the iris; so that after it has been completely removed, a radial contraction in the remainder, if it occurred, would not be a very striking phenomena. A radial shortening, although not arresting attention like the contraction of the sphincter, can however always be made out in the ciliary part of the iris on placing it in warm salt solution; if the ciliary region is already somewhat retracted, the radial shortening may only show itself by the piece becoming curved, the shortening in fact is then confined to the posterior layer, and this at the edge partially draws away from the anterior layer so that the anterior layer projects over the posterior. A better way of showing the radial shortening is by cutting a radial strip of the whole iris, extending this gently in cool salt solution, and then placing it in warm salt solution.

The difference between the sphincter and ciliary region of the iris is then simply one of degree; contraction with warmth is incomparably a more striking phenomenon with the sphincter than with the radial strip, but the behaviour of the radial strip is not inconsistent with the existence of a radial muscle.

Roy[1] has shown that warmth causes a retraction of elastic tissue; but that the shortening of the radial strip is not caused by elastic tissue is shown by its much greater amount in favourable circumstances, and by its disappearing one to two days after death, at a time when the properties of elastic tissue are unaltered.

[1] Roy. This *Journal*, Vol. III. p. 125, 1881.

(*b*) *Electrical stimulation.* Grünhagen[1] on suspending a strip of the ciliary portion of the iris, found no change in its length on directly stimulating it. Later however Hurwitz[2] under Grünhagen's direction and with an improved form of the instrument previously used, obtained shortening of a strip of the ciliary region of the iris kept at 28°—30° C., on sending induction shocks through it. Grünhagen does not however regard this as proof of the existence of a radial muscle; possibly he considers the contraction as being due to the out-curving bundles of the sphincter, which according to him serve with a contracted sphincter to constrict the pupil. Moreover Hurwitz found no radial contraction in the ciliary portion of large ruminants, he obtained it only in the irides of the rabbit and the cat.

2. **Elongation of the excised sphincter on stimulation.** The important discovery that the tone of the sphincter can be diminished by direct stimulation is due to Grünhagen and Samkowy[3] (1875). They cut out the sphincter, suspended it between two hooks, connected the lower hook with a lever, warmed the strip to cause it to contract, and then stimulated it, usually with induction shocks sent from end to end of the strip. They found in certain cases that the result was not contraction but elongation of the sphincter.

In the rabbit's sphincter, stimulation normally caused a contraction followed by an elongation past the original point; occasionally elongation only was obtained. Atropin had no effect upon the result. With the cat's sphincter they usually obtained pure elongation, and always if atropin had been given. Grünhagen[4] (1880) notices that these effects are only obtained on the sphincter when it has been removed from the body.

It is not certain whether the elongation thus produced is due to a direct stimulation of the muscle-cells or to a stimulation of nerve-endings, Grünhagen has pointed out that the elongation can be obtained for some hours after death, and this suggests a direct action on the muscle, but it is not conclusive, for possibly the nerve-endings retain their irritability long after the nerves in connection with them have ceased to be irritable.

If it were shown that the elongation is due to stimulation of nerve-

[1] Grünhagen. *Arch. f. d. ges. Physiol.* Bd. x. p. 172, 1875.

[2] Cp. Grünhagen. *Arch. f. d. ges. Physiol.* Bd. xxxiii. p. 59, 1884. In this paper, Grünhagen gives a brief account of the dissertation of Hurwitz (1878), Biernath (1882), Pfalz (1882). We quote from this account.

[3] Grünhagen u. Samkowy. *Arch. f. d. ges. Physiol.* Bd. x. p. 165, 1875.

[4] Grünhagen. *Transactions Internat. Med. Congress* (London) Vol. i., p. 269, 1881.

endings, the fact would go far to prove that the sympathetic is an inhibitory nerve for the sphincter. For the evidence is against either of the other nerves which supply the iris having this function. After atropin has been given, the third nerve has no effect on the pupil, but it does not prevent the elongating effect of direct stimulation of the excised sphincter. And there is no satisfactory evidence that stimulation of the fifth nerve, centrally of the Gasserian ganglion, causes dilation of the pupil.

It must be noted, however, that even if the sympathetic were shown to be capable of inhibiting the sphincter, that would not exclude the possibility of its also being capable of causing a radial muscle to contract.

The experiments mentioned in this section we have not repeated.

3. **Comparison of the latent period of constriction with that of dilation.** It was remarked by Budge (*op. cit.* p. 85), that, commonly, contraction of the pupil followed stimulation of the third nerve more promptly than dilation followed stimulation of the sympathetic. François-Franck[1] using weak stimuli noticed a considerable difference in this respect; he considers this difference to be in favour of the view that the action of the sympathetic is an inhibitory one. But, as he himself mentions, the difference might be due to the sphincter muscle having more tone than the dilator, and this naturally would cause a delay in the manifestation of the contraction of a radial muscle.

As a matter of fact, the difference in the latent period of contraction and dilation of the pupil depends chiefly upon the strength of the stimulus; and a strong stimulation of the sympathetic will cause a dilation of the pupil more quickly than a weak stimulation of the third nerve will cause a contraction. Furthermore, even if the latent period of the sympathetic were always the greater, it would still remain to be shown that this is a characteristic of peripheral inhibitory action.

4. **Analogy.** It has been argued and chiefly by Gaskell[2], that the general anatomical and physiological relations of the sympathetic system indicate that its pupillo-dilator fibres are inhibitory. But one of the chief arguments urged in favour of this, viz. that motor and inhibitory nerves run a different course and are connected with nerve-

[1] François-Franck. *Travaux de la Laboratoire de M. Marey*, 1878—1879, published 1880, p. 1.

[2] Gaskell. This *Journal*, Vol. VII. p. 37, 1886.

cells in different ganglia, has not stood the test of experimental observation. Both motor and inhibitory nerve-fibres are connected with nerve-cells in the superior cervical and in other sympathetic ganglia.

Analogy leads us very little way in determining whether the sympathetic fibres running to any particular tissue are motor or inhibitory. The sympathetic fibres to the heart are motor, those to the intestine are chiefly, at any rate, inhibitory. The sympathetic fibres to the blood-vessels of the salivary glands are, so far as is known, motor only; those to the blood-vessels of the ear are chiefly motor, though some apparently are inhibitory; those to the bucco-facial region are certainly in part motor and in part inhibitory.

Stimulation of the cervical sympathetic, besides causing dilation of the pupil, causes protrusion of the eye, and retraction of the nictitating membrane. All of these movements are antagonized by stimulation of the third nerve. Yet the action of the sympathetic upon the protrusion of the eye, and the retraction of the nictitating membrane can easily be shown to be due to a muscular contraction, and not to inhibition. Analogy, then, so far as it is worth anything, is in favour of the dilation of the pupil being also due to a muscular contraction.

ON THE RELATION BETWEEN THE VASCULAR CHANGES IN THE IRIS AND THE SIZE OF THE PUPIL.

We have already pointed out that in estimating the effect of vaso-motor nerves on the size of the pupil, the state of turgescence of the vessels is the only factor which has usually been considered, but that the dilation might be due to a longitudinal contraction of the arteries. These two views we shall consider separately.

1. **Turgescence of the blood-vessels of the iris.** Before the discovery of the action of the sympathetic upon the pupil, or rather, before any attention was given to this discovery, it was believed by many that the movements of the pupil were due to variations in the amount of blood in the vessels of the iris. And it was noticed, that when an injection mass was forced into the blood-vessels, the iris became smaller. This view was, however, disproved by the observation that in man the blood-vessels of the head and eye might be gorged although the pupil was dilated, and that after death by decapitation the pupil became small, although the blood had drained from the vessels[1].

[1] Cp. Hyrtl. *Hdb. d. Topograph. Anatomie*, 1847, p. 149.

A similar line of observation shows, that the dilation which follows stimulation of the sympathetic can be produced independently of a diminution in blood supply to the iris.

This was shown fairly conclusively by the experiments of Budge and Waller[1] (1851), and of Budge (1855). It is true that Budge and Waller did not make their experiments with any view to the theory we are now considering; vaso-motor nerves were in fact then undiscovered. But they found that stimulation of the sympathetic for some time after death caused dilation of the pupil; since there was no arterial blood-pressure, and since the stimulation was repeated more than once, it is in the highest degree unlikely, that variations in the amount of blood in the iridic vessels could have been the cause of the dilation of the pupil. The experiment, with varying degrees of regard for the points to be attended to, has often been made in later times and perhaps most satisfactorily by François-Franck (1880), who after bleeding an animal to death, stimulated the sympathetic at intervals several times in succession, obtaining each time dilation with intervening return to the constricted state.

The observation is easily made, and further evidence is offered by the fact that dilation can be produced in an extirpated eye by stimulating a long ciliary nerve.

Although it is certain that the sympathetic is capable of causing a dilation of the pupil in some other way than by decreasing the amount of blood in the iris, it seems, on general grounds, reasonable to suppose that variation in the state of turgescence of the blood-vessels of the iris should have a not inconsiderable effect; and this view is widely believed. Nevertheless, it appears to us that the view has no satisfactory foundation, and that the tone of the muscular part of the iris is sufficient normally to prevent the tendency to movement due to variations in the amount of blood in the iris. Waller[2] pointed out that pressing the eye of a white rat so as to make the iris bloodless had no effect on the pupil. The considerable variation in blood-pressure caused by stimulating the central end of the depressor, or the lower cut end of the spinal cord, usually causes no alteration in the size of the pupil. Brown-Séquard[3] noticed that injecting blood into the ophthalmic artery caused but a barely appreciable constriction of the pupil. We have injected a

[1] Budge et Waller. *Comptes Rendus de l'Acad. des Sciences*, T. XXXIII. p. 418, 1851.

[2] Waller. *Comptes Rendus de l'Acad. des Sciences*, T. XLIII. p. 659, 1856.

[3] Brown-Séquard. *Journal de la Physiologie*, II. p. 452, 1859.

mixture of blood and warm salt solution into the carotid, at minimal and at very high pressures, with results similar to those of Brown-Séquard, great variation in the pressure caused either no effect or a trifling constriction or a trifling dilation. When carmine injection mass was substituted for the normal salt solution, there was a considerable constriction of the pupil, even if the pressure were low. Clearly, the constriction of the pupil in this case was due to a stimulation of the sphincter. On the other hand, if an eye is taken two or more days after death, as in some of Mosso's[1] experiments, and the vessels are injected, variations in the size of the pupil may follow the variations in the pressure of the injected fluid.

2. **Contraction of the blood-vessels of the iris.**

Bernard[2] in 1852 found that stimulation of the cervical sympathetic caused pallor in the ear and in some other parts of the head.

Waller[3] in 1853 observed similar effects and definitely attributed them to a direct action of nerve-fibres in the sympathetic on the coats of the arteries, i.e. to vaso-motor fibres. The existence of vaso-motor nerve-fibres for the iris was first established by Kuyper[4] (1859) working under Donders; he observed pallor of the iris in albino rabbits on stimulation of the cervical sympathetic.

Since there are in the iris a number of radial arteries, a dilation of the pupil might be caused by a contraction of these arteries. It is extremely improbable that the sympathetic could cause a contraction of the longitudinal coat of the arteries without causing at the same time a contraction of the circular coat; so that—for the present at any rate—observations which show that the sympathetic dilation of the pupil is independent of arterial constriction may be taken as showing that it is also independent of a longitudinal contraction of the arteries.

The consideration of the facts relating to this matter may for the sake of clearness be divided into sections.

(*a*) *Simultaneous observation of the size of the pupil and of the condition of the blood-vessels in some other part of the head than the iris.*

A good many observations coming under this section have been made, for animals with unpigmented irides are not always readily obtainable, and as they are either rabbits or rats, they are only adapted for certain kinds of experiment.

[1] Mosso. *Hofmann und Schwalbe's Jahresbericht*, 1875, II. p. 79.

[2] A. Bernard. *Comptes Rendus de la Soc. de Biol.* 1852, p. 169.

[3] Waller. *Comptes Rendus de l'Acad. des Sciences*, T. XXXVI. p. 378, 1853.

[4] Cf. Donders. *Accommodation and Refraction of the Eye* (The New Sydenham Society), p. 530, 1864.

The observations taken together show conclusively that by stimulating the cervical sympathetic, or certain portions of it, a dilation of the pupil may be obtained without evoking a contraction of the blood-vessels of the ear or of the retina. And if we may safely deduce from the absence of contraction of the vessels of the ear and retina, that there is also an absence of contraction of the vessels of the iris, the independence of the sympathetic dilation of the pupil and the vascular contraction in the iris is amply demonstrated.

But this is a deduction which we think cannot be safely made.

With regard to the retina, there is, indeed, much difference of opinion as to what effect stimulation of the cervical sympathetic has on its circulation. Most observers have failed to find any effect. Jegorow[1] in the rabbit finds constriction. Doyon[2], in the cat and dog, finds dilation. We have not come to any decisive conclusion on the point, but in most cases we have failed to observe any alteration of the retinal vessels to follow sympathetic stimulation.

Nevertheless since much stress has been laid on observations of this kind, we give an account of them here, together with some additional observations of our own.

Arlt[3], working under Donders, found that on stimulation of the cervical sympathetic in rabbits, the time of beginning, maximum, and ending of the dilation of the pupil and of the contraction of the vessels of the ear did not correspond. François-Franck observed a similar lack of correspondence, taking a tracing of the pressure in the peripheral end of the carotid instead of observing the vessels of the ear.

The cervical sympathetic is usually composed of two or more bundles of nerve-fibres. Schiff[4] (1872) found that occasionally he could cut one of these bundles, leaving the other intact, and by so doing deprive the part of the sympathetic centrally of the cut of its action on either the blood-vessels of the ear, or on the dilation of the pupil and movements of the eye. And he concluded that one bundle contained all the vaso-motor fibres for the head and another contained all the oculo-pupillary fibres.

A more constant separation of the pupillary from the vaso-motor fibres has been described by François-Franck[5]. It was shown by Budge and

[1] Jegorow. *Archiv f. Anat. u. Physiol.* (Physiol. Abth.) 1886, p. 174.

[2] Doyon. *Arch. de Physiol. norm. et path.* 1890, p. 774; 1891, p. 154.

[3] Arlt, Junior. *Archiv f. Ophthalmologie,* xv. p. 294, 1869.

[4] Schiff. (Quoted from François-Frank, *op. cit.*)

[5] François-Frank. *Travaux de la Laboratoire de M. Marey,* 1880.

Waller (*op. cit.* 1851) that the pupillo-dilator fibres after leaving the superior cervical ganglion accompanied the internal carotid artery in the internal carotid canal, leaving it to run to the Gasserian ganglion. According to François-Franck, the superior cervical ganglion gives off two strands to the carotid canal, and the external strand causes dilation of the pupil but no increase in pressure in the peripheral end of the carotid, whilst the other strand, breaking up into a plexus over the internal carotid artery, causes increase of pressure in the peripheral end of the carotid without any dilation of the pupil.

François-Franck also states that the pupillo-dilator fibres run exclusively in the anterior limb of the annulus of Vieussens, whilst the vaso-motor fibres run in both the anterior and the posterior limbs. We are not quite clear as to François-Franck's position with regard to this statement, for though on p. 29 and 30 (*op. cit.*) it is made without reserve and as having no exception, on p. 7 (*op. cit.*) it is apparently said to be of rare occurrence.

We have made a few experiments on this point—two on the dog and two on the cat—and have in each case found oculo-pupillary fibres in the posterior limb of the annulus of Vieussens. The response evoked by it is less[1] than that evoked by stimulating the anterior limb of the annulus; but there is a similar though less marked difference between the effect of the two limbs of the annulus on the blood-vessels of the ear.

A third place in which François-Franck finds a separation of the two kinds of nerve-fibres, is in the short ciliary nerves. Some of these cause constriction, others dilation of the pupil, but with neither did François-Franck observe any variation in the retinal vessels, or any variation in the intra-ocular pressure.

Jegorow[2] (1886) took the condition of the vessels of the retina as an indication of the state of constriction or dilation of the vessels of the iris. He found in the dog, after section of the vago-sympathetic trunk, that stimulation of the central end of a sensory nerve caused a slight dilation of the pupil, but no change in the vessels of the retina or of the ear; that after section of the long ciliary nerves, stimulation of the central end of the vago-sympathetic caused no dilation of the pupil, but caused strong contraction of the vessels of the retina and of the ear; and that stimulation of the peripheral end of a single long

[1] In our experiments stimulation of the posterior limb of the annulus on the right side in the cat, though causing prompt dilation of the pupil never caused maximum dilation.

[2] Jegorow. *Archiv f. Anat. u. Physiol.* (Physiol. Abth.) 1886, p. 149.

ciliary nerve caused dilation of the pupil without alteration in the vessels of the retina. Jegorow also states that neither atropin nor eserin cause any change in the blood-vessels of the retina.

Langley and Dickinson[1] (1890) noticed that after injecting various poisons—and especially brucin—into the blood of a rabbit, stimulation of the cervical sympathetic sometimes caused complete constriction of the vessels of the ear, but no dilation of the pupil.

Lastly there is evidence of a difference in origin from the spinal cord of the vaso-motor fibres for certain parts of the head and the oculo-pupillary fibres. Bernard[2] (1862) observed in the dog, that section of the roots of the 1st and 2nd thoracic nerves caused dilation of the pupil, but no vascular change in the skin of the head, whilst section of the thoracic sympathetic between the 2nd and 3rd rib caused dilation of vessels of the head on the same side, but no dilation of the pupil. Since cutting off a portion only of the nerve-supply to a tissue does not usually give rise to appreciable paralytic symptoms, Bernard's experiment must only be taken as showing that the majority of the pupillo-dilator fibres are contained in the 1st and 2nd thoracic nerves, and that the majority of vaso-motor fibres for the head arise from some other source. Later observers have attempted to ascertain more accurately the origin from the spinal cord of vaso-motor and pupillo-dilator fibres. According to the latest observations by Langley[3] the dilator fibres for the pupil arise, in the dog, cat and rabbit, from the first three thoracic spinal nerves; whilst the vaso-motor fibres for the head arise in the dog and cat from the 1st to the 5th thoracic nerve, and in the rabbit from the 2nd to the 8th thoracic nerve. Further the 1st thoracic nerve in the cat sometimes caused maximum dilation of the pupil without causing any contraction of the vessels of the ear. In the rabbit paling of the conjunctiva was seen on stimulating the 4th thoracic, and slight paling on stimulating the 5th thoracic nerve, although neither of these nerves caused dilation of the pupil.

If, now, the vaso-motor nerves for the iris have the same origin from the cord as the vaso-motor nerves for the ear, the experiments just mentioned are sufficient to demonstrate that sympathetic fibres can cause contraction of the vessels of the iris without causing any dilation of the pupil. It seemed to us advisable to make some experiments on this point. We have stimulated the thoracic sympathetic (one cat and

[1] Langley and Dickinson. This *Journal*, Vol. XI. p. 519, 1890.

[2] A. Bernard. *Journ. de la Physiol. de l'Homme etc.* T. V. p. 383, 1862.

[3] Langley. *Phil. Trans. Royal Soc.* B. p. 103, 1892.

two albino rabbits) from about the 6th thoracic ramus upwards to the ganglion stellatum, previously cutting the rami communicantes in this region. We have also stimulated the last cervical and the upper thoracic nerves in the spinal canal (two albino rabbits). During the stimulation, the pupil, the blood-vessels in the ear and the blood-vessels in the iris were observed. With the albino rabbit a microscope was used for a part of the time to observe the circulation in the iris; the observation is rather tiresome, and is only satisfactory in a bright light. In rabbits with pigmented irides, and in the cat, the arteries of the major circle, and a certain number of the chief radiating arteries can be readily seen with a hand-lens. On stimulating the thoracic sympathetic below the 3rd white ramus there is more or less complete constriction of the arteries of the ear, but we have not been able in any case to see a distinct and indubitable constriction of the arteries of the iris. In some cases, when the stimulus was applied to the thoracic sympathetic between the 3rd and the 5th white ramus, there was also more or less complete contraction of the arteries of the conjunctiva, but still without any certain contraction in the arteries of the iris. But when the sympathetic was stimulated at the lower end of the ganglion stellatum—so that dilation of the pupil occurred—the iridic arteries contracted until they were lost to view[1].

Stimulation of the nerve-roots in the spinal canal gave corresponding results. Marked and considerable constriction of the arteries of the iris only occurred on stimulating the first three thoracic nerves, i.e. the spinal nerves which also cause dilation of the pupil. This result is the more striking since the 1st thoracic nerve produced no effect whatever upon the arteries of the ear[2].

Great constriction and after-flushing of the arteries of the ear were caused by the 2nd, 3rd, 4th and 5th thoracic nerves; moderate constriction and after-flushing by the 6th, and a slight constriction or slight flushing by the 7th nerve. There appeared to be a trifling constriction of the arteries of the iris on stimulating the 4th and 5th nerves without any dilation of the pupil.

Notwithstanding, however, that dilation of the pupil and distinct constriction of the vessels of the iris were caused by the first three

[1] It sometimes happens that in exposing the thoracic sympathetic the circulation in the head on the operated side is considerably retarded or diminished. In such cases the iris is much more quickly injured than the vessels of the ear; stimulation of the cervical sympathetic may cause complete constriction of the vessels of the ear, but have no effect on the pupil.

[2] Cp. Langley. *Phil. Trans. Royal Soc.* B. p. 103, 1892.

thoracic nerves and by these only, the readiness and extent of the pupillary dilation was not proportional, with the several nerves, to the readiness and extent of the arterial constriction.

We conclude then that the state of the vessels of the ear or of the conjunctiva cannot be taken as an indication of the state of the vessels of the iris. And that the origin of the vaso-motor fibres for the iris corresponds with the origin of the dilator fibres for the pupil, and not with that of the vaso-motor fibres for the ear.

(b) *Simultaneous observation of the size of the pupil and of the condition of the blood-vessels of the iris in circumstances other than stimulation of the sympathetic.*

Waller[1] (1856) noticed in the white rat, that during the dilation of the pupil caused by atropin, there was no contraction of the iridic arteries. The vessels became zigzag or spiral, and remained full of blood. Vulpian[2] (1873) repeated the experiment with similar results.

This observation is important and has received less attention than it deserves. It shows that a large dilation of the pupil can be obtained apart from any contraction of the vessels of the iris. It is true that atropin has usually been supposed to be without effect on blood-vessels, but the bearing of this upon the vascular theory of dilation seems to have been unrecognized.

Since, however, the sympathetic can cause a dilation after atropin has been given, there still remains a possibility of dilation by vaso-motor action.

An observation on similar lines is that of Hamer[3] working under the direction of Donders. He found in albino rabbits, that after a small dose of eserin had been applied to the eye, stimulation of the cervical sympathetic produced pallor of the iris, but little or no dilation of the pupil. This result, however, might be explained by the contraction of the sphincter being too strong in the conditions of the experiment to be overcome by the contraction of the arteries.

We have made one or two experiments with eserin ; in the rat, after local application of eserin to the eye, the sympathetic had no effect upon the pupil, it caused slow constriction of the vessels of the iris, on cessation of the

[1] Waller. *Comptes Rendus*, T. XLIII. 1856, p. 659.

[2] Quoted from François-Franck (*op. cit.*) p. 10, note.

[3] Cf. Donders. *Accommodation and Refraction of the Eye*, p. 580, 1864.

stimulus the vessels rapidly dilated; in the cat, eserin did not annul the action of the sympathetic on the pupil.

When stimulating the 4th to the 8th thoracic nerves in albino rabbits in the spinal canal, we have noticed at times, when there were indications of slight escape of current to the spinal cord, most of the possible forms of independence between the movements of the iris and the contraction of its blood-vessels. Thus we have seen a slow constriction of the pupil both without any change in the vessels of the iris and with a slight contraction of them. We have also seen, a quick rhythm of complete contraction and full dilation of the arteries set up, the later contractions and dilations taking place with a perfectly unmoving pupil. In these cases the effects produced are no doubt reflex.

In albino rabbits a flushing of the iris accompanied by a dilation of the pupil may sometimes be caused by gently pinching the skin. We give an account of an experiment in which this was observed. This experiment is remarkable because stimulation of the cervical sympathetic caused a constriction of the pupil. This occurred constantly when the electrodes were placed close to the cut end of the nerve, and only when they were placed there. The constriction may have been reflex and due to the presence of a few vagus or other cerebral nerve-fibres running with the sympathetic.

Experiment I.

Rabbit. Small albino. Give $\frac{1}{2}$ gram chloral hydrate by rectum; later inject $1\frac{1}{2}$ c.c. 2 p.c. morphia under skin.

12.23 Left cervical sympathetic tied and cut. The left ear and conjunctiva flush, the mucous membrane of the mouth shows no change, both already pink; the iris, if it changes at all, becomes slightly paler.

12.30 Stimulate sympathetic; s.c. at 9 (shocks rather weak to tongue); —iris, conjunctiva and ear become pale; the pupil constricts a little, and on cessation of the stimulus dilates to its previous size.

12.33 Repeat stimulation—same result.

12.35 Stimulate sympathetic farther away from the cut end; s.c. at 10;—the ear becomes pale and the pupil dilates.

Reflect sunlight into the eyes—the pupil constricts and the iris becomes paler.

Stimulation of the sympathetic at the cut end of the nerve gives constantly a slight constriction of the pupil and a slight paling of the iris; the pupil dilates on ceasing the stimulation.

12.46 Stimulate sympathetic; s.c. at 8; if the electrodes are placed on the cut end the pupil constricts, if placed elsewhere on the nerve, the pupil dilates; after the end of the stimulation the iris becomes very pale, without any movement of the pupil.

12.55 Pinch gently the skin of the chest—the iris at once becomes red and the pupil dilates. Repeat several times with the same result.

(c) *Simultaneous observation of the size of the pupil and of the condition of the blood-vessels in the iris produced by stimulating the sympathetic.*

We have quoted above (p. 575) an experiment of François-Franck's on the effect of stimulation of the external branch given off to the carotid canal by the superior cervical ganglion. He found that stimulation of this branch caused dilation of the pupil without causing constriction of blood-vessels in certain regions of the head. It appears also from his account—though it is not very clear—that in one or more experiments he examined the iris with a lens, and noticed no contraction of its vessels notwithstanding the dilation of the pupil.

Our observations have been made in the first place on rabbits with unpigmented irides, the cervical sympathetic was stimulated and the circulation in the iris watched with a microscope.

In the albino rabbit, the radiating vessels have a sinuous or spiral course, unless the pupil is very small. On stimulating the sympathetic so as to obtain dilation of the pupil and contraction of the arteries, it can easily be seen that—as in the atropin dilation described by Waller—the vessels become markedly more sinuous or spiral, and at places of bifurcation, the angle of bifurcation becomes greater.

As the pupil dilates the circular arteries become straighter and where they divide in a circular direction, the branches become more closely pressed together. When the pupil is large, many radial arteries may, unless much dilated, be hidden by the circular folds of the anterior surface of the iris.

The dilation of the pupil cannot, then, be due to a longitudinal contraction of the blood-vessels, except on the supposition that longitudinal muscular fibres form a more or less spiral thickened strand around the arteries. And of this there is no evidence under the microscope.

Further proof is offered by the absence of synchronism between the movements of the pupil and the change in calibre of the blood-vessels. When the cervical sympathetic is stimulated for a second or two only,

there is dilation of the pupil without any appreciable contraction of the vessels of the iris. On the stimulation of the sympathetic for a longer time, the vessels of the iris do not begin to contract until the maximum dilation of the pupil is nearly or even quite attained; and on cessation of the stimulus, the greater part of the constriction of the pupil is over before the dilation of the blood vessels begins. If the stimulation is much prolonged the iris begins slowly to constrict, although the vessels show no sign of dilation, but after cessation of the stimulus, the return to normal is quicker with the blood vessels than with the pupil. There is in fact a similar difference in the time of dilation of pupil and constriction of blood vessels of the iris to that found by Arlt and by François-Franck in the time of dilation of the blood vessels of the ear. We must, however, expressly state that on stimulating the cervical sympathetic, the contraction of the vessels of the iris, and the contraction of the vessels of the ear are often not synchronous; so that the state of the vessels of the iris cannot be safely deduced from the state of the vessels of the ear.

The independence of the two actions of the sympathetic on the iris can also be seen in the albino rabbit after injecting brucin (cf. above p. 576). It is true we have not obtained after giving brucin complete abolition of the action of the sympathetic on the pupil, with retention of its action on the blood vessels of the iris. But we obtained a stage in which the sympathetic caused a momentary slight dilation only of the pupil at the beginning of the stimulation and this was followed by complete pallor of the iris unaccompanied by a change in the pupil. When in this stage the sympathetic was stimulated two or three times in quick succession, the second or third and later stimulations caused no dilation of the pupil. Making use of this fact we could obtain complete contraction of the arteries of the iris without any change in the size of the pupil.

In the white rat the circulation in the iris can be seen better than in the rabbit; and, as in the rabbit, there is little difficulty in showing that the sympathetic causes dilation of the pupil in some other way than by causing a contraction of the vessels of the iris. We give a sketch of the arteries of a portion of the iris of a rat (*a*) before (*b*) after a momentary stimulation of the sympathetic (Fig. 8).

In the albino rabbit and white rat, all the arteries of the iris examined under the microscope contracted and dilated simultaneously[1]

[1] When a constriction of the iridic arteries is brought about reflexly, the arteries of the major circle and the arteries radiating from it to the sphincter border do not necessarily constrict and dilate synchronously.

so that we think the arteries which, in the pigmented iris, are visible with a hand lens afford a satisfactory indication of the state of all the iridic arteries.

We have in consequence made additional observations upon rabbits with pigmented irides and upon cats. The results are similar to those

a b

Fig. 8. Diagram of branching radial vessels in part of the iris of the rat (*a*) pupil small, (*b*) pupil fairly large; after momentary stimulation of the sympathetic.

already given for the albino rabbit and need not be repeated here. In the cat when the sympathetic is stimulated with a weak current the prompt dilation of the pupil and the slow contraction of the arteries is very marked. The chief drawback to this as an easy demonstration experiment is that at a certain stage of dilation of the pupil, the arterial major circle disappears more or less completely under the edge of the sclerotic.

Possible connection between the ciliary muscle and the size of the pupil. On the supposed inhibitory action of the sympathetic upon the ciliary muscle.

The continuity of the iris with the choroid coat suggests that a movement backward or forward of the choroid coat caused by variation in the state of contraction of the ciliary muscle might cause some though not great variations in the size of the pupil. It is to be noticed, however, that the variations in the size of the pupil produced in this way would tend to be counteracted by the synchronous forward or backward movement of the anterior surface of the lens.

According to Flemming[1] and others a slip of the ciliary muscle is in some animals as in the cat and dog attached to the outer part of the iris, so that its contraction would cause some dilation of the pupil, and its relaxation some constriction of the pupil.

The evidence with regard to the action of the cervical sympathetic

[1] Flemming. *Arch. f. mik. Anat.* Bd. IV. p. 372, 1868.

on the ciliary muscle is conflicting. Jessop[1], observing the phakoscope images on the lens, was unable to see any alteration in them on stimulating the sympathetic. On the other hand, Morat and Doyon[2] state in the most positive manner that stimulation of the cervical sympathetic causes a flattening of the lens in dogs, cats and rabbit. They observed the size of the image thrown on the lens by an obliquely placed light, and—in two cases in dogs—the movement of a needle thrust through the cornea and resting on the lens. They consider that the sympathetic contains inhibitory fibres for the ciliary muscle.

We have experimented on dogs and cats in three ways; either (*a*) a strip of the sclerotic was cut away just behind the ciliary attachment, and the choroid directly observed or (*b*) a needle was passed through the edge of the cornea so that its point rested upon the surface of the lens, and the head and the point of the needle observed or (*c*) the lenses of a phakoscope were fixed in a board and arranged so as to throw two images on the surface of the lens. In the last method we have made also one or two observations on the rabbit. Contraction of the ciliary muscle was caused by morphia or by pilocarpin, or by stimulating the 3rd cranial nerve in the skull.

On stimulating the cervical sympathetic, we did not observe the slightest movement of the choroid or any backward movement of the lens. With the phakoscope images our results are the same as Jessop's; we have not observed, as a result of sympathetic stimulation, any enlargement of the images on the lens, or any increase in the distance between them. A change in the images is of course caused by every movement of the head of the observer; and a certain degree of modification may be caused by the contraction of the orbital membrane, for the contraction produces a bulging of the eye, and may alter the direction of its axis. Taking the precautions which these facts suggest, we have observed repeatedly, on stimulation of the sympathetic, completely immobile images whilst the pupil passed from a small size to maximal dilation.

As a control, we have commonly stimulated the 3rd cranial nerve in the skull. In these cases the needle method readily showed a forward movement of the lens. The phakoscope images in the dog and cat when viewed very obliquely, are easily seen to advance towards

[1] Jessop. *Proc. Roy. Soc.* Vol. XL. 1886, p. 478; *Bericht ü. d.* VII. *Internat. Ophthal. Congress*, 1888, p. 188. Jessop states that when the ciliary muscle is moderately contracted e.g. by pilocarpin, it relaxes on stimulation of the long ciliary nerves.

[2] Morat et Doyon. *Arch. de Physiol. norm. et path.* 1891, p. 507.

the cornea; the images, when viewed less obliquely become closer together and somewhat smaller.

The approximation of the images is, however, very much less than that which occurs in man in accommodating for near objects.

Taking all our experiments together, we are forced to conclude, that the sympathetic is not an inhibitory nerve for the ciliary muscle[1].

In two cases in the dog, stimulation of the sympathetic caused constantly a slight forward movement of the lens (needle method used); we attribute this to the pressure exercised on the eye by the contraction of the unstriated muscle of the orbital membrane.

Experimental proofs of the existence of a radial contractile substance (dilator muscle) in the iris.

We have shown in the preceding sections that no increase of any importance in the radial tension of the iris can be produced by a contraction of its blood vessels, or by a relaxation of the ciliary muscle.

In this section we bring forward proof that an increase in radial tension together with a shortening can nevertheless be produced in any given radial strip of the iris. It is obvious that such a change cannot be due to a contraction, local or otherwise, of the sphincter, and the form of the experiments precludes it from being due to a relaxation of the sphincter.

The only other possible explanation is that there is a contractile substance radially disposed in the iris which by its contraction leads to a dilation of the pupil. This contractile substance we shall speak of, now and then, as the dilator muscle. This term, however, we use simply for convenience. For our histological observations, so far as they have gone, do not by any means satisfy us that the contractile substance is in the form of unstriated muscular fibres. This question we shall discuss in our later paper.

1. **Movement of the iris on the side opposite to a local dilation.** Whenever a marked local dilation is produced, whether by local stimulation of the sclerotic, or by stimulation of the cervical sympathetic,—the long ciliary nerves save one being cut—the side of the iris opposite to the stimulus is more or less dragged over to the stimu-

[1] As we have mentioned above, in all our experiments the animals were anæsthetized. Just before the actual stimulation, curari also was given to paralyze the motor oculi muscles. We think the anæsthetic condition important, for with imperfect anæsthesia there is a possibility of reflex inhibition of the 3rd nerve.

lated side. This is readily seen in any of the various ways in which slight movements of the iris can be observed. It must be remembered however that this does not necessarily occur unless the dilation is really confined to one spot; when, as not infrequently happens on stimulating the sclerotic, there is a general dilation of the pupil, in addition to the local dilation, the effects described in this section may not be noticeable.

In Fig. 9 are represented the forms of the pupil in the rabbit, (*a*) at rest, (*b*) on stimulating the sclerotic on one side, (*c*) on stimulating the sclerotic on opposite sides. The vertical lines represent the hair lines in a scale fixed over the eye, and through which the pupil was observed.

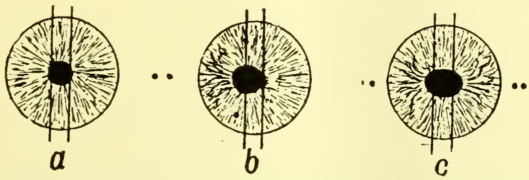

FIG. 9. Diagrams of iris of rabbit, to show movement of the iris on the side opposite to that stimulated towards the stimulated side. The dots outside the iris, represent the position of the electrodes, (*a*) iris at rest, (*b*) iris stimulated on one side, (*c*) iris stimulated on opposite sides.

In the cat, in which the contracted pupil is a vertical slit, one or both ends of the slit are dragged across the median line, on stimulating the part of the sclerotic facing the side of the slit (cp. Fig. 10).

FIG. 10. Diagrams of iris of cat (*a*) at rest, (*b*) on local stimulation of sclerotic. In (*b*) the upper angle of the pupil has been dragged from the mid-line towards the part stimulated.

In the dog, after morphia has been given, the pupil as is well known is circular and very small,—on stimulating the sclerotic with strong currents the pupil becomes spindle-shaped; and the whole pupil, still small, is perceptibly, although very slightly, dragged towards the side stimulated; with attentive observation, the dragging movement can be seen in the ciliary portions of the iris most remote from the stimulating electrodes.

It is impossible, we think, to account for these facts on the theory that the movements of the iris are produced solely by a sphincter muscle capable of being inhibited, and of radial elastic fibres. In such a system a relaxation of any part of the sphincter causes recession of all parts of the iris from the centre.

2. **Local dilation of the pupil with simultaneous local contraction of the sphincter.** The effects to be described here we have studied chiefly in the cat[1]; they can be observed also in the dog, but in order to observe them satisfactorily, morphia should not be amongst the anæsthetics used, since this causes too great a contraction of the pupil; in the rabbit the effects are very slightly marked.

When, in the manner of Jegorow, a local dilation of the pupil is obtained in the cat on stimulation of the cervical sympathetic, that is after section of all save one of the long ciliary nerves, the portion of the iris corresponding to the dilation moves evenly outwards, the movement is purely in a radial direction unmixed with any movement which could suggest a contraction of circularly arranged muscles. In consequence of the radial shortening, circular folds appear on the anterior surface of the iris, starting at the ciliary border and increasing in number with increasing dilation.

The local dilation which occurs on applying the electrodes to the edge of the sclerotic is with minimal currents and with currents a certain degree above minimal, of the same nature. But with stronger currents the movement of the iris is less simple, in addition to the outward radial motion there is a drawing together of the iris on either side of, and towards the most dilated portion. There is in fact a contraction of the sphincter, as well as a shortening of the radial diameter of the iris. The contraction of the sphincter is very obvious; indeed when the iris is examined with a lens or with a microscope, this contraction is as obvious as the dilation of the pupil; it is at its maximum at the most dilated portion of the pupil, and on either side of this becomes less and less, though stretching half way round the iris if the stimulus used be strong.

The contraction of the sphincter naturally causes a different set of folds in the pliable anterior surface of the iris, the folds start closely packed together from the edge of the pupil in a radial direction and

[1] Grünhagen (*Zeitschrift f. rat. Med.* Bd. XXVIII. p. 275, 1866) mentions an experiment in which stimulation of the sclerotic caused simultaneously local contraction of the sphincter and local dilation of the pupil; after atropin, dilation only was produced. This is the only mention of the fact we have been able to find.

then curve outwards, diverging as they go (cf. Fig. 11), and rapidly becoming indistinct.

The contraction of the sphincter and the radial outward movement do not, as a rule, with moderately strong currents, either begin or end

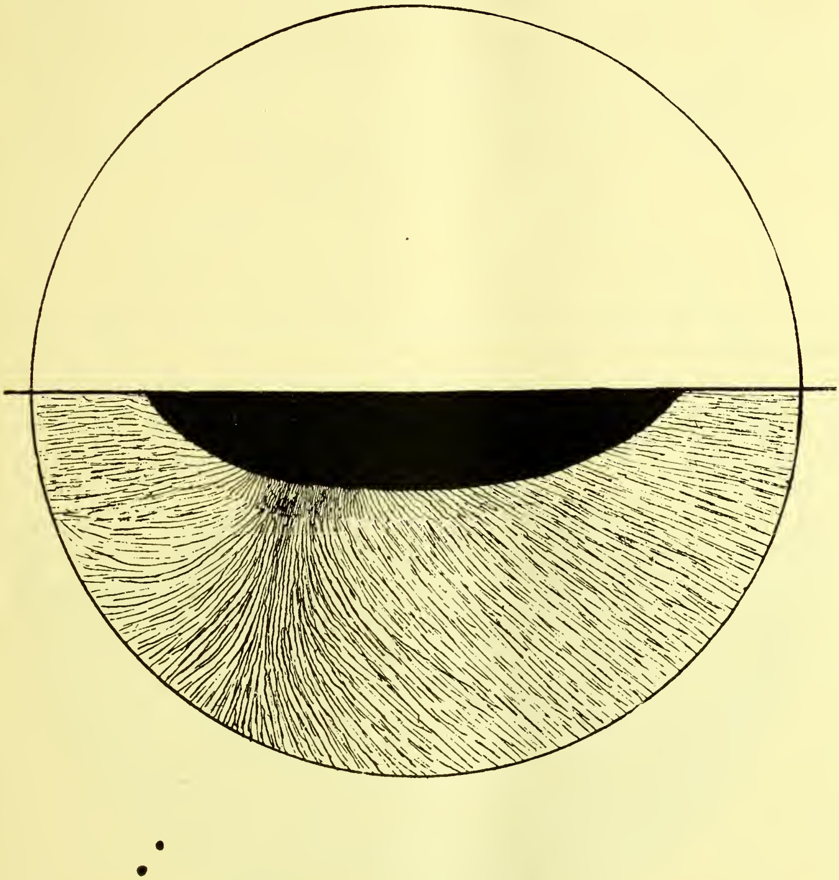

FIG. 11. Diagram of effect of local stimulation of the sclerotic in the cat. 1st stage. Contraction of the sphincter. The two dots indicate the position of the stimulating electrodes.

simultaneously. With strong currents they may apparently begin simultaneously, with currents just sufficient to stimulate the sphincter we have occasionally seen the radial movement before the contraction of the sphincter, but we have not paid much attention to the changes except those produced by moderate or moderately strong currents. With such currents we find, in nearly all cases two stages, which we have endeavoured to represent in Figs. 11 and 12.

The first effect of stimulation is usually a slight brief contraction of the pupil[1]; immediately after or as a continuation of this contraction, the inner edge of the iris opposite the electrodes gathers into fine radial folds or creasings and the portion of the iris on either side passes towards this region, thus increasing the number of folds. The shifting of the inner border of the iris is further indicated by the curved course taken by the folds. The first stage, which is caused by the contraction of the sphincter is shown in Fig. 11.

Whilst the sphincter is still contracted, and before it has attained its

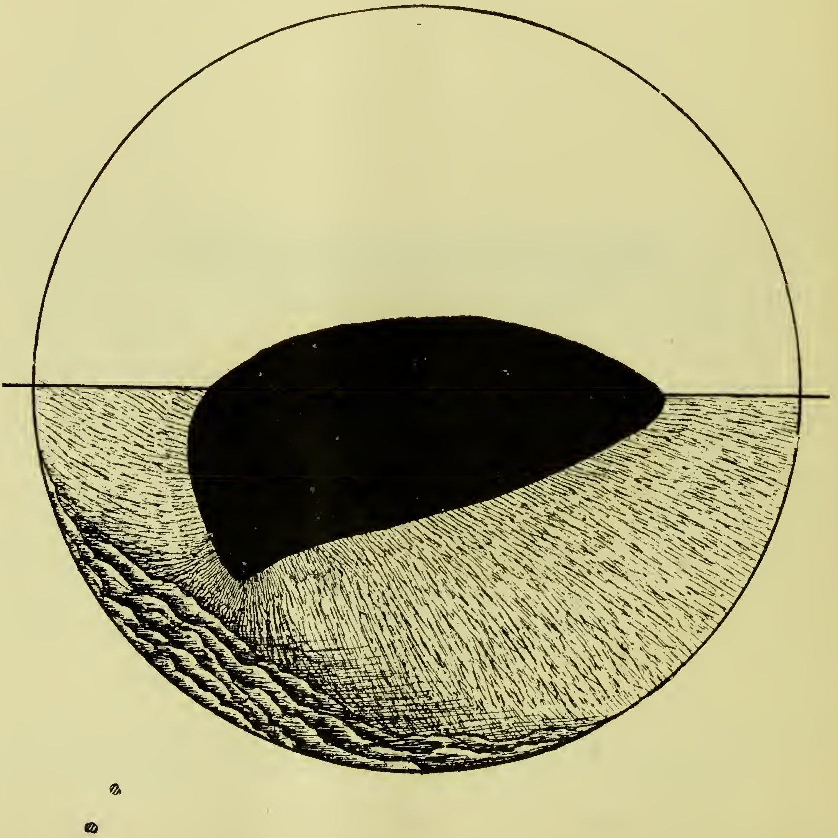

FIG. 12. Diagram of effect of local stimulation of the sclerotic in the cat. 2nd stage. Radial contraction superposed upon the contraction of the sphincter.

[1] This is not always seen, its absence is probably due to the simultaneous action of the dilator muscle. The prominence of the sphincter contraction varies with trifling variations of the position of the electrodes on the sclerotic. In fact the constrictor and dilator nerves appear to run to a certain extent separately even in the anterior part of the sclerotic.

fully contracted condition, the local dilation of the pupil begins; circular folds[1] are seen at the ciliary border of the iris increasing in number as the dilation increases. The iris of the opposite half is more or less distinctly dragged towards the stimulated side. This second stage is shown in Fig. 12.

On cessation of the stimulus, the effects disappear in the reverse order to that in which they commenced. The contraction of the sphincter ceases first, and the radiating lines seen on the surface of the iris run straight outwards instead of being curved; then there is a

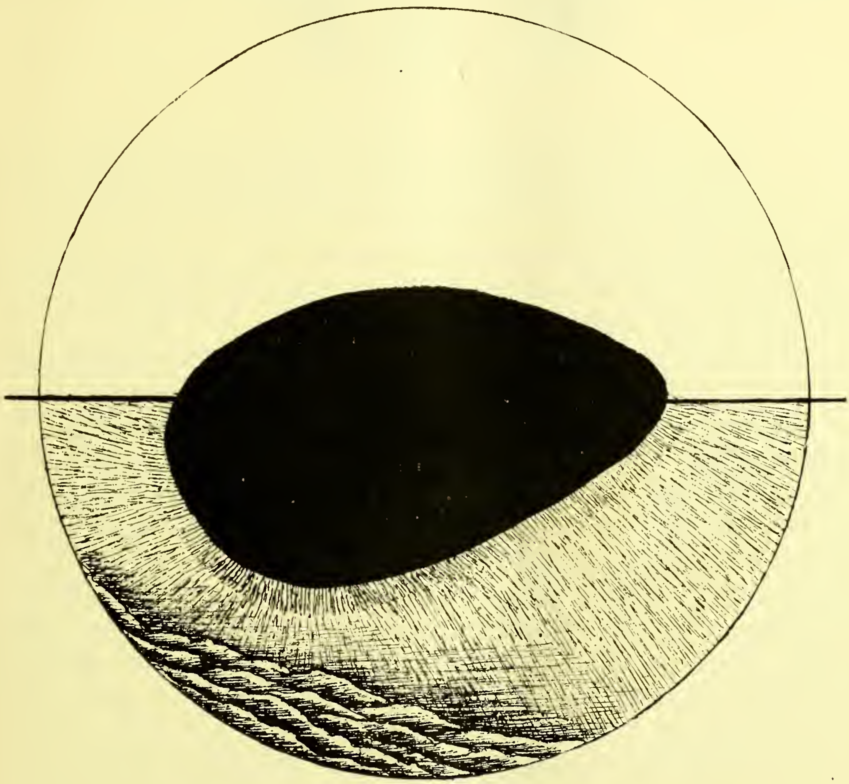

Fig. 13. Diagram of the appearance of the iris shortly after ceasing to stimulate the sclerotic. Relaxation of sphincter, with slight diminution only of the radial contraction.

slight lessening of the circular folds, the shape of the pupil becomes less irregular (Fig. 13), the extended opposite side of the iris passes

[1] These folds are large and very unlike the fine radial creasings caused by contraction of the sphincter muscle.

back to its normal position; finally there is a more gradual disappearance of the circular folds and the pupil returns to its original shape.

We have seen a similar series of changes in the iris of the dog, on stimulating a single ciliary nerve near its entrance into the sclerotic. As a rule, in these stimulations, the contraction of the sphincter is not accompanied by a local bulging of the iris on the pupil side, but this does sometimes occur. An example of this we give in Fig. 14. In

Fig. 14. Diagram of changes in cat's iris, sometimes seen on local stimulation of the sclerotic (*a*) local contraction of sphincter, the contracted part bulging into the pupil, (*b*) subsequent local dilation of pupil, the contracted sphincter having been dragged outwards.

Fig. 14 (*a*), the sphincter is contracted and bulges into the pupil, in Fig. 14 (*b*) the radial pull has come into play and dragged outwards the still contracted sphincter.

We do not think that there can be any question with regard to the main fact in the above account, viz. that a dilation of the pupil may occur in a part of the iris in which the sphincter is strongly contracted. It follows that in this case, the dilation of the pupil cannot be caused by an inhibition or by a relaxation of tone of the sphincter. We have seen (p. 561) that a local inhibition of the sphincter might cause a local dilation. A local contraction of the sphincter[1] causes a diminution in the size of the pupil; in the case mentioned above, this is not only counteracted but the pupil becomes larger than normal. The only possible explanation is that there is an increased radial pull and this as we have seen above[2] can only be due to the contraction of a radial arranged substance or radial muscle.

3. **Contraction of a radial strip of the iris.** If two radial cuts close together are made in the iris, a wedge shaped piece of iris is obtained isolated from the rest except at its outer or ciliary region. In such a radial strip, the contraction or relaxation of the portion of sphincter muscle in it, may cause a slight narrowing or widening of the

[1] This can be obtained by stimulating a single short ciliary nerve, the contraction is, however, much less local than that which can be obtained by stimulating the sclerotic.

[2] There is no difficulty in seeing that the local dilation begins before the contraction of the iridic arteries.

pupillary edge, but cannot cause any radial movement either inwards or outwards of the whole piece.

We have observed the behaviour of such a strip of the iris in different conditions in the rabbit, cat, and dog. The cornea is cut away causing more or less constriction of the pupil; the radial cuts are made; as a result of this the strip shortens; the rest of the iris retreats towards the ciliary border so that the strip is left lying free on the lens somewhat as in Fig. 15.

Fig. 15.

It will be noticed that in the figures the radial cuts do not stretch up to the ciliary border; the object of this is to avoid cutting the outer circular artery of the iris (circulus arteriosus major); for when this is cut the bleeding is very profuse, and the movements of the strip of iris cease sooner. We would expressly mention, however, that the effects we are about to describe can be obtained when the radial cuts pass to the outer limit of the iris, or even if the cuts be prolonged through the sclerotic and choroid past the ciliary processes.

In the strip of iris described above, a radial shortening can be produced by direct stimulation, by stimulating the sclerotic, and also, and this is more important, by stimulating the cervical sympathetic.

After each radial shortening, the strip of iris must of course be extended, perhaps the best way of doing this is to brush it from ciliary to pupillary edge as it lies on the lens; if it be stretched by pulling on the pupillary edge with a fine forceps, care must be taken not to overstretch it. And it is advisable to leave an interval of two or three minutes between the successive stimuli.

The radial shortening of the strip is by no means equally well seen in the three animals we have experimented on.

In the rabbit it is very slight, and is usually only seen for a minute or two after removing the cornea, in one or two cases, however, the sympathetic has caused a radial shortening for half-an-hour after exposure. We are not quite clear why the effect is so slight or why it should cease so soon. But in connection with this it must be borne in mind that stimulation of the 3rd nerve has also as a rule but a slight and sluggish effect on the sphincter, after the cornea has been removed.

In the dog, the effects are usually striking, though not of long duration, but we have obtained the best and most constant effects on the cat. A certain amount of variation in effect is to be expected, according to the extent to which the radial cuts sever the nerve-fibres supplying the strip. As the nerves form a wide-meshed plexus in the iris, some severance of nerve supply is unavoidable on making radial cuts.

Seen at its best, the shortening of the strip is very striking, it is easily seen without magnification, and proceeds until the strip is a half or less than a half of its previous length. If the strip has been extended by brushing it over the lens, it occasionally sticks for a moment and then comes away with a jerk, rapidly shortening. Although stimulation of the sympathetic, after removal of the cornea, usually causes some protrusion of the lens, the shortening of the radial strip of iris takes place whether there is or is not such protrusion. It can be seen when the surface of the eye is flooded with salt solution; in this case however there is usually a tonic contraction of the strip so that naturally there is less scope for visible contraction.

In the cat, we have examined the strip during its contraction, using a microscope magnifying sufficiently to show the circulation of the blood. It can be seen that during contraction, the blood vessels become bent, and do not undergo any appreciable longitudinal contraction, sometimes also no appreciable decrease in diameter.

Successive pieces of the strip proceeding from the pupillary edge may be cut away, and similar effects less in extent are still obtained; and after cutting away three-quarters of such a strip of the cat's iris, we have still obtained shortening of the remainder on stimulating the sympathetic.

Tracings of the shortening of the strip of the iris may also be obtained by tying a fine silk thread to the edge, passing the thread over a wheel and connecting it with a light lever, but the experimental difficulties are considerable, for the force exerted by the radial strip is very slight, and by the time all the apparatus has been properly adjusted, the sympathetic may have ceased to produce an effect.

When the sympathetic ceases to cause radial shortening, direct stimulation also is as a rule without effect. Occasionally on applying a fine pair of electrodes to the edge of a strip, a shortening is seen almost entirely confined to the part stimulated, whether this be in the pupillary or ciliary zones. Occasionally also on turning the strip back so as to expose its posterior surface, local stimulation of the posterior

surface will cause small local waves of contraction. Finally if the strip be thus turned back, and the sphincter edge fixed, stimulation of the sympathetic will often cause distinct local areas of contraction in the outer (ciliary) portion of the posterior membrane of the iris, sometimes the contraction appears to travel as a wave from the outer to the inner (pupillary) part.

4. **Absence of elasticity from the iris.** The inhibitory theory of the action of the sympathetic pre-supposes that the iris contains elastic tissue capable in the absence of opposing force of producing the fullest dilation of the pupil. As the iris, in maximal dilation almost disappears under the edge of the sclerotic, the unstretched state of the iris means on this view a very short radial diameter. This aspect of the question has been much disregarded. It is true that Grünhagen states that if the sphincter of a rabbit's iris be removed, the remaining portion retracts to a narrow rim. This obviously might result from a contraction of a radial muscle, for in such an experiment, the cut-off sphincter ring also usually contracts. But putting this on one side, it not infrequently happens that in such an experiment the retraction of the outer portion is slight, and if the eye be left in the body for two or more days (when warm salt solution no longer causes a contraction of the sphincter) no retraction at all takes place in the ciliary portion of the iris on removing the sphincter. That is to say the retraction is not produced by elastic tissue.

Further suppose two radial cuts are made in the iris, and the piece between the cuts retracts; if this be gently stretched and held so for a minute or so, or if it be several times gently extended by brushing it, it will in most cases remain for a time extended instead of retracting at once as stretched elastic tissue would. In the cat and dog it at once retracts on tapping, or otherwise stimulating it.

This behaviour is incompatible with the view that the dilation of the pupil is due to elastic tissue in the iris.

On the supposed inhibitory action of the sympathetic upon the sphincter iridis.

We have seen above that the sympathetic is capable of bringing about a dilation of the pupil by causing the contraction of a radial tissue; it is conceivable that this action should be aided by a simultaneous inhibition of the sphincter. We have made experiments to determine this upon the rabbit, cat, and dog by three somewhat similar methods.

In the first method the cornea is removed, the pupil widened and distorted in shape, and the time and manner of its return to its normal shape noted; the distortion of the pupil is then repeated, and immediately afterwards the cervical sympathetic is stimulated, the time and manner of the return of the pupil to its normal shape again noted. This method is not quite satisfactory, because of the radial contraction which takes place on stimulating the sympathetic, but so far as it goes, it gives no indication that the sphincter is inhibited.

In the second method, we have taken a strip of the iris, in the manner described on p. 591. In such a strip, the sphincter edge is more or less contracted, in the cat and dog this is marked by fine radial lines over the sphincter and by a narrowing of the sphincter portion; in the rabbit, the sphincter portion often becomes sharply marked off from the rest of the iris.

On stimulation of the cervical sympathetic, there is not the faintest sign of relaxation of the sphincter edge, although there is, as we have said earlier, more or less radial shortening.

In the third method, the eye is fixed, the slit of the pupil (in the cat) is prolonged by two radial cuts in the iris; so that the iris is cut into halves; one half is taken and the sphincter tied at either end with a fine silk thread; one silk thread is fixed, the other is passed over a wheel and fastened to a light lever the pointer of which is nearly in contact with a vertical millimetre scale. With this arrangement an elongation of the sphincter by itself will cause a fall of the lever[1]. On stimulating the sympathetic, however, the lever rises; this is easily seen to be due to the radial contraction of the piece. In order to avoid the movement caused by the radial contraction, two needles are passed through the iris, a little distance from the pupil edge and fixed, so that a radial movement is prevented.

In no case have we been able to observe any sign of inhibition of the sphincter as the result of stimulating the sympathetic; although we have varied the weight of the lever, and although we have experimented with various degrees of contraction of the sphincter, caused partly by exposure, partly by dropping upon it warm salt solution.

We conclude then that the sympathetic has no inhibitory power on the sphincter muscle.

In connection with this we may mention some experiments we have

[1] Instead of a lever we have sometimes used a thin strip of wood with torsion suspension. In order to prevent reflex movements of the eye, curari is given in addition to anæsthetics.

made with the 3rd nerve. So much of the unstriated muscle of the body is supplied with inhibitory as well as with constrictor nerve-fibres, that there is a prima facie probability that all the unstriated muscle of the body is supplied with inhibitory nerve-fibres. Since we had failed to find inhibitory fibres for the sphincter in the cervical sympathetic, and since constrictor and inhibitory fibres often run together, it seemed to us worth while to observe carefully the action of the 3rd nerve.

We have carefully stimulated the 3rd nerve in the skull with induced currents of varying strength and of varying rate, and with the direct battery current of varying strength and interrupted at varying intervals. But we have never found any other effect than constriction of the pupil, except when there were indications of escape to the 5th nerve.

SUMMARY.

We append a brief abstract of the line of argument of the preceding paper, and of the chief facts dealt with in it. The other points which we have considered may be gathered from the 'contents' given at the beginning of the paper.

The proofs which have been brought forward up to the present time as to the way in which the sympathetic causes dilation of the pupil are inconclusive.

For a dilator muscle it has been said :—

That the spincter muscle dies at a time when the cervical sympathetic nerve will still cause a dilation of the pupil (Budge). The rapid death of the sphincter postulated here, was shown by Brown-Séquard not to occur.

That the occurrence of a local dilation of the pupil (Bernstein and Dogiel, Engelhardt, Jegorow) shows the presence of a radial muscle. It might however, be produced by local contraction of blood vessels, or by local inhibition of the sphincter muscle.

That dilation of the pupil in the rabbits may be obtained after removal of the sphincter (Kölliker). But this might be due to a contraction of the blood vessels of the iris, or possibly to a mechanical bulging of the lens.

Against a dilator muscle it has been urged :—

That the ciliary portion of the iris does not contract with warmth like the sphincter portion; (Samkowy and Grünhagen). This is true but the difference is only one of degree.

That the sphincter can be made to dilate by direct stimulation (Grünhagen and his pupils) and that probably the sympathetic acts in a similar way and inhibits the sphincter (François-Franck, Gaskell). The conclusion is not more than a probability, and no direct proof of such action of the sympathetic has been brought forward.

In favour of the sympathetic dilation of the pupil being brought about in some other way than by an action of the blood vessels it has been urged :—

That on stimulation of certain nerves, the contraction of the blood vessels of various parts of the head does not occur synchronously with the dilation of the pupil, and that probably the blood vessels of the iris contract simultaneously with the other blood vessels of the head (Arlt, Schiff, François-Franck, Jegorow). In fact, however, the contraction of the blood vessels in the iris cannot be safely judged from the state of the blood vessels in the other parts of the head.

That atropin causes dilation of the pupil in white rats without causing any constriction of the blood vessels (Waller). This does not show how the sympathetic causes dilation.

Reviewing the whole of the previous observations, we think they show a probability that the sympathetic causes a dilation of the pupil, not by producing a contraction of the blood vessels, but partly by causing a contraction of a dilator muscle and partly by causing an inhibition of the sphincter muscle.

We have endeavoured to bring forward decisive proof on these points.

A direct examination of the iris during the stimulation of the cervical sympathetic shows that the pupil dilates before the vessels contract, and assuming that the longitudinal muscular coat of the arteries contract simultaneously with the circular coat, the experiment shows that the sympathetic dilation of the pupil is not due to a contraction of the blood vessels.

It can be shown also that some radially arranged contractile substance exists in the iris for when local dilation of the pupil passes a certain limit, the opposite side of the iris is dragged towards the stimulated side, this local dilation is not produced by an inhibition of the sphincter muscle, for the sphincter muscle can be made to contract locally at the same time, its contraction being greatest at the most dilated portion of the pupil. Further, stimulation of the sympathetic causes shortening of a radial strip of the iris, isolated from the iris on either side of it, and this shortening may be obtained before or without any contraction of the blood vessels in it ; and on examining the

posterior surface of the iris, small waves of contraction may be seen on its posterior surface when the sympathetic is stimulated.

There is also proof of the absence of elastic tissue in the iris; a radial strip does not always retract on being stretched as it would do if it contained elastic tissue, and if the iris be left until its muscular tissue is dead, a radial strip of it does not shorten as it would if the sympathetic dilation of the pupil were due to elastic tissue pulling outwards an inhibited sphincter.

We have not found any evidence that the sympathetic can cause an inhibition of the sphincter muscle, it causes radial shortening of a portion of the iris without the least trace of relaxation in the tone of the sphincter border.

But notwithstanding the proof that a radial contractile substance exists in the iris, we have not satisfied ourselves that it has the form of ordinary unstriated muscular tissue, and this question we reserve for a later paper.

Note.

To p. 574. *Action of the sympathetic on retinal vessels.* Morat and Doyon (*Archiv de Physiol. norm. et path.*, 1892, p. 60) in a Paper which we had overlooked when writing the above, find that the cervical sympathetic, though causing flushing of the retina in the cat and dog, causes pallor of the retina in the rabbit (cp. Jegorow, *supra*).

They further find in the rabbit, that, after section of the 5th cranial nerve, stimulation of the cervical sympathetic causes constriction of the vessels of the conjunctiva and sclerotic, but very little dilation of the pupil and no alteration in the retinal vessels.

May 31, 1892.

A brief statement of some of the chief results of this paper was made to the Physiological Society on May 14, and published in the July number of this *Journal.*